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Ecological drivers of hunter-gatherer lithic technology from the Middle and Later Stone Age in Central Africa

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ABSTRACT

Central Africa is a key region for examining patterns of hunter-gatherer inhabitation and engagement with ecological diversity and environmental change. In contrast to adjacent regions, however, the archaeological record of prehistoric hunter-gatherer populations in Central Africa is underrepresented in studies of recent human evolution. This limited engagement with Central African archaeological records in part stems from the complexities of identifying, excavating, and dating hunter-gatherer sites in what are today often heavily forested environments, a focus on named stone tool industries from undated sites to structure the record, and highly limited means to associate dated hunter-gatherer occupations with proxy records of environmental conditions. Here, we present a novel synthesis of prehistoric hunter-gatherer stone tool assemblages from dated Central African sites and use climate model datasets to illuminate the environmental and ecological landscapes in which they were deployed. Our results suggest a significant ecological shift occurred from 14,000 years ago onwards, associated with a greater engagement with broadleaf forests. We examine the extent to which a range of geographic and paleoclimatic drivers can explain patterns of gross assemblage composition and the appearance of individual lithic technologies highlighting the significant role of changes in altitude, precipitation, seasonality, and ecology. Notably, considerable continuity can be observed between the habitat ranges of contemporary hunter-gatherer populations in Central Africa and prehistoric occupations that significantly precede the appearance of farming lifeways in the region.

1. Introduction

Central Africa remains severely underrepresented in studies of human evolution. This is largely the result of a limited availability of human fossils and archaeological remains in this area, particularly in contrast to other regions of the continent. This scarcity of evidence is partly due to the prevalence of humid and acidic soils that prevent the preservation of fossil material (Capriles et al., 2019; Foley, 2018), as well as the difficulties in identifying sites with high integrity Quaternary sediment sequences in the currently forested habitats of the region. Historically, this has been compounded by the widespread belief that human populations would have not been able to subsist in the tropical rainforest environments that currently dominate the region before the advent of agriculture (Bailey, 1991; Rosas et al., 2022), facing challenging conditions including high heat and humidity (Hewlett and Cavalli-Sforza, 1986), high structural density (Diamond, 1991), high densities of certain pathogens (Guernier et al., 2004), and low food availability especially in certain seasons (Hart and Hart, 1986). Recently, however, this has been challenged by research that has begun to clearly demonstrate successful Late Pleistocene adaptation to tropical habitats and specialised exploitation of rainforest resources (e.g. Barker et al., 2017; Bourgon et al., 2021; Wedage et al., 2019). Archaeological records show that humans did occupy Central Africa tens of thousands of years prior to the origins of agriculture in the region (e.g. Cornelissen, 2002; Mercader et al., 2002; Taylor, 2014). The growing appreciation of the polycentric appearance of key features of behavioural adaptation as well as the significance of population structuration between regions within Africa to understand present genetic variability (Scerri et al., 2018) places a new emphasis on the need to understand the structure of archaeological records from overlooked regions of the continent.

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Contemporary Central African hunter-gatherers possess some of the most divergent human genetic lineages, with studies estimating a separation from other human populations between 100 and 120 thousand years ago (ka) (Bergström et al., 2021; Fan et al., 2019; Schlebusch and Jakobsson, 2018) (but see (Lipson et al., 2020)). Moreover, the human remains that do exist from which ancient DNA has been extracted (in the Shum Laka cave in Cameroon) indicate a genetic continuity in the region (Lipson et al., 2020, 2022), as well as extremely high morphological diversity (at Ishango Cave in the eastern) (Crevecoeur et al., 2016; Twiesselman, 1958). Hunter-gatherer groups living in East and West Central Africa are thought to have diverged from one another 50–70 ka (Fan et al., 2019), but recent research suggests that these two distinct groups would have maintained regular connectivity (Padilla-Iglesias et al., 2022a,b; Wang et al., 2020) possibly facilitated by ecological conditions. Ecological analyses based on the locations on niches occupied by contemporary populations suggest considerable continuity in the habitability of Central Africa by hunter-gatherers since the last interglacial, focusing on habitats characterized by low temperature and precipitation seasonality and a combination of rainforest and tropical savanna biomes (Padilla-Iglesias et al., 2022a).

Today, Central Africa is inhabited by both farming and foraging populations living in close association with one another. All Central African hunter-gatherers now speak languages coming from farming populations, and exchange of subsistence goods and technologies is widespread (Hewlett, 2017). The appearance of farming lifeways in Central Africa, tied closely with the concept of Bantu expansions, is well documented (Bostoen et al., 2015; Clist, 2022; de Saulieu et al., 2021; Fortes-Lima et al., 2023; Garcin et al., 2018; Grollemund et al., 2015, 2023; Koile et al., 2022; Oslisly et al., 2013; Russell et al., 2014; Seidensticker et al., 2021). The cultivation of *Pennisetum glaucum* (Pearl millet) and *Elaeis guineensis* (Oil palm) and other oil-rich fruits such as *Canarium*, starts becoming widespread between 2.2 and 2.4 ka with slash-and-burn agriculture and yam cultivation probably practiced in the region much earlier (Cagnato et al., 2022; Neumann et al., 2012, 2022).

From ca. 3 ka, habitation sites of farming populations are found in forest contexts, associated with lithic industries, followed by the appearance of iron production ca. 2.8–2.6 ka (Breunig, 2014; Clist, 2013, 2022), with some debate as to when or whether stone tool technologies were abandoned (Clist, 2006a; Lupo et al., 2015; Mercader and Brooks, 2001). Prior to the expansion of farming populations, evidence for the use of ceramics extends back to more than 7ka at Shum Laka (Lavachery, 2001). At this site, four potsherds were found in a layer dated to 7ka, whilst more abundant pottery started appearing from 5ka onwards (Lavachery, 2001). While considered the product of a foraging population, the early appearance of pottery at Shum Laka could be indicative of subsistence changes associated with the greater durability of storage vessels, though differential visibility in the archaeological record may also be a factor. Moreover, the analyses of ancient DNA extracted from four hunter-gatherer individuals buried in Shum Laka cave dated to ca. 8 ka and 3 ka indicate that although the four of them have genetic profiles most related to today's Central African hunter-gatherers, they might have already carried a significant proportion of ancestry from a source related to the ancestors of contemporary east African agro-pastoralists. This might indicate that hunter-gatherers inhabiting the rock shelter were already interacting with people practicing other means of subsistence. Nonetheless, genetic analyses cannot determine this, and there is currently no evidence for the presence of agro-pastoralism in Central Africa at that time (Hsieh et al., 2016; Li et al., 2014; Lipson et al., 2020; Lopez et al., 2018; Mitchell and Lane, 2013; Vicente and Schlebusch, 2020). Evidence of mid-Holocene pottery use by Central African hunter-gatherers is also found in Chavuma (Zambia) and Sablières (Gabon) (Phillipson, 1976; Clist, 1995; Jordan et al., 2016). After that, evidence of pottery use by hunter-gatherers is found much later ca. 3ka in the Nangara-Komba rock shelter in the Central African Republic (Lupo et al., 2021) Faunal collections from a few pre-agricultural sites that are today located within the forest are indicative of savanna or savanna/woodland environments (Bailey and Headland, 1991), offering some insight into subsistence economies. Beyond this, our understanding of prehistoric hunter-gatherer populations in Central Africa is based upon stone tool assemblages, how they change through time, and the locations from which they have been recovered.

Extensive survey work has identified a large number of sites yielding stone tool from across Central Africa (Braucher et al., 2022; Barham and Mitchell, 2008; Casey, 2005; Clist, 1995; Cornelissen, 2002; D'Andrea and Casey, 2002; Lanfranchi et al., 1991; Mercader, 2002a, 2002b; Mercader and Brooks, 2001; Taylor, 2011; Van Noten, 1982); however, comparative studies of lithic technologies from this region, and elsewhere, face a number of challenges. In particular, Taylor (2011) highlights key problems with site taphonomy, frequently impacted by fluvial reworking, and the confidence with which a relationship between chronometric dating of a site and the recovered stone tool assemblage can be asserted as a result (Braucher et al., 2022; Cahen, 1976; Cahen, 1978b). In the absence of clearly resolved chronologies, a range of different taxonomic nomenclatures have been used to describe the stone tool industries of Central Africa, including the Sangoan, Lupemban, and Tsitholian, alongside more generic description of Middle and Late Stone Age assemblages, to structure the archaeological record (Cahen, 1978b). The Sangoan has typically been viewed as either a transitional industry following the Acheulean or an early facies of Middle Stone Age industries, typified by the prominence of heavy tool elements in Sangoan assemblages such as core-axes or picks, and historically found in tropical habitats that are currently forested (e.g. Clark, 1964; Guédé, 1995; Lanfranchi, 1991; Sheppard and Kleindienst, 1996) though recent evidence suggests a greater ecological and geographic spread (e.g. McBrearty, 1992; Van Peer et al., 2003). Sangoan assemblages with robust geochronological constraints remain rare (Duller et al., 2015). Lumpemban assemblages are almost unique to Central Africa and best known for the presence of large bifacial foliates, alongside diverse bifacial, prepared core, and blade reduction strategies (Taylor, 2016). Resolving their chronological placement or relationship to more generic instances of MSA technologies in the region is not straightforward, with the majority of sites in the region dating between 45–20 ka, which may be a constraint imposed by the limitations of radiocarbon dating, in contrast to U-series dating at Twin Rivers where Lupemban deposits are dated to 270–170 ka (Barham, 2002; Taylor, 2016). The Tsitholian is considered by some to mark a significant change in technological practice and a shift toward microlithic toolkits, alongside the continued use of some larger tools (Lanfranchi et al., 1991; Van Neer and Lanfranchi, 1985), whereas generic LSA assemblages are reported combining microliths, backed artefacts and blade production, appearing broadly from 30 to 20 ka (Brooks and Robertshaw, 1990; Brooks and Smith, 1987; De Heinzelin, 1957; Mercader and Brooks, 2001). The prevalence of large cutting tools in the region has typically been attributed to requirements of inhabiting forested habitats, though this is not clearly supported by direct proxy evidence for these tools types associated with forests in the Pleistocene, with palaeobotanical evidence available only in rare instances from archaeological sites (e.g. Shum Laka). Despite the somewhat disparate nature of the available archaeological record, researchers have identified a continuity of lithic technologies throughout the late Pleistocene and Early Holocene of Central Africa (Cornelissen, 2002, 2013; Mercader and Brooks, 2001).

The composition of stone tool assemblages, like the wider archaeological record, is shaped not only by the behaviour of past populations but also through the actions of archaeologists in the present and recent past, both of which must be accounted for when undertaking a synthesis. Indeed, modern academic, political and environmental contexts can play a significant role in forming our understanding of the human past, as can the scale of research activity, such as the size of excavations undertaken. Previous research has elucidated the ways in which past human behaviour can be identified from lithic artefact assemblages (e.g.

Andrefsky, Jr, 2005; Shea, 2016). This encompasses the detail of mechanical and technological procedures undertaken in the diverse reduction trajectories employed to create an assemblage (e.g Li et al., 2022), direct evidence for patterns of stone tool use from function studies (Marreiros et al., 2015), as well as reflecting on how the formation of stone tool assemblages can reflect patterns of human engagement across their landscape, including patterns of raw material access and use, mobility, and where sites occur with respect to alternate resource bases (e.g. Clarkson, 2007; Tostevin, 2012). While the overarching goals of lithic assemblage analyses may be broadly shared, discrete differences occur in the methods employed and how they tackle precise questions regarding past behaviour, both within and between major research traditions (e.g. Pargeter et al., 2023; Scerri et al., 2016; Will et al., 2019). This significantly complicates comparative studies undertaken between researchers from different traditions as they have evolved across any given region's research history, and the questions that can be approached through synthesis.

In Central Africa, numerous studies do present detailed and insightful analyses of individual stone tool assemblages that offer rich insight into past human behaviour at the site level (e.g. Lavachery, 2001; Mesfin et al., 2021). However, the absence of a single analytical framework for such studies substantially limits the current potential for inter-site comparisons. Performing a macroscale analysis of a large region over a considerable period necessarily involves omitting some detail. Qualitative descriptions of reduction technologies and retouched tool forms have been ubiquitous features of studies of stone tool assemblages, including those in Central Africa, presenting the means to undertake the broadest synthesis (e.g. Kandel et al., 2023). Elsewhere in Africa, common typological terms for lithic artefacts have served as the basis of both descriptive and analytical regional syntheses (e.g. Basell, 2008; Blinkhorn and Grove, 2018; Kandel et al., 2016; Niang et al., 2023; Scerri and Spinapolica, 2019; Tryon and Faith, 2013). Inconsistencies in terminology (including multiple instances of approximately synonymous terms), together with the sparsity that would be created if all original published designations were retained, suggests that the amalgamation of terminologies into a consistent, broad classification is essential. Such amalgamation avoids further confusion over terminology, ensures analytical tractability, and allows conclusions to be drawn at the appropriate scale. The manifestation of archaeological patterning at different scales should be a central focus of research, as has now been recognised in many parallel disciplines (e.g. Perreault, 2020). Notably, from this common basis, such studies have been able not only to provide concise descriptions of regional records built up over decades of research, but also investigate questions about past patterns of mobility, ecological engagement and the role of cultural transmission in mediating technological diversity.

Here we present a current synthesis of dated stone tool assemblages of prehistoric Central African hunter gatherers, examine behavioural variability within this dataset, and explore the extent to which behavioural differences can be explained with respect to differences in space, time, geography and ecology. The extended spatio-temporal scale employed below is necessary to elucidate any patterns in the dataset due to chronology, geography, or both; and, given the sparsity of archaeological assemblages (in terms of both their number and their composition), it has the additional benefit of providing a dataset amenable to statistical analysis. In doing so, we illuminate the wealth of data that is available from the region and capitalize upon the availability of palaeoclimate and palaeoecology simulations at high spatio-temporal resolution to tackle gaps in the availability of proxy records from archaeological sites. In particular, this synthesis of archaeological and model datasets provides a means to examine the extent to which ecology, and particularly the prevalence of forests, has structured past human behaviour in Central Africa, and to identify patterns that can be tested with ground-truthing in future studies. The scale of analysis employed here achieves all the benefits highlighted above, but this certainly does not imply that this is the only scale at which these assemblages could be analysed; the same is true of the terminology and the analytical methods employed. Indeed, elsewhere comparable methods have been employed to examine intra- and inter-assemblage variability in metric attribute datasets (Blinkhorn et al., 2021). We undertake this synthesis to explore variability in Stone Age records of Central Africa on its own terms as presented in the literature, but with a view to facilitating future multi-scalar analyses within Central Africa and comparisons between adjacent regions.

2. Dataset

We compiled information on dated stone tool assemblages with lithic material from Central Africa, spanning 8 countries (Republic of Congo, Democratic Republic of Congo, Gabon, Cameroon, Central African Republic, Zambia, Equatorial Guinea, Angola) from the Middle Stone Age onwards from the primary literature, excluding sites with clear taphonomic issues following recent reviews of the regional radiocarbon dated catalog (Clist et al., 2023; Garcin et al., 2018; de Saulieu et al., 2021; Seidensticker et al., 2021) and regional syntheses (Cornelissen, 2013, 2016). For each assemblage we recorded site geographic coordinates, whether sites were located in open or closed (rock-shelter or cave) contexts, details of chronometric dating, and the catalogue of cultural materials reported.

In order to focus on stone tool assemblages produced by hunter-gatherer populations, we excluded assemblages reported in the literature as "Neolithic", "Early Iron Age" or "Recent Iron Age", as well as those in which *Pennisetum glaucum* (Pearl millet), *Elaeis guineensis* (Oil palm), iron metallurgy or pit features were apparent (following Garcin et al., 2018; Seidensticker et al., 2021). Although worldwide the use of ceramic pots by hunter-gatherers is both widespread and ancient (see for example Budja, 2016; Clist, 1995; Jordan et al., 2016; Lupo et al., 2021) some authors question the place of pottery use within hunting and gathering subsistence economies (Testart et al., 1982). Therefore, we also noted those sites for which there was evidence of pottery use, but for which no other evidence associated with agricultural lifeways were present. In our dataset, the oldest evidence of pottery use is found in Shum Laka rock shelter in Cameroon, associated with a C14 date of 7140 ±40 (Utc-8026) which returns a calibrated age of 7.868–8.021 cal BP(de Maret et al., 1987; Lavachery, 2001). This broadly coincides with genomic-based estimates of the earliest date of admixture between hunter-gatherers from Western Central Africa and agriculturalist populations. We argue that this presents a conservative approach to dataset building in the Central African context, which is likely to exclude recent hunter-gatherer sites in which use of metal tools and consumption of agricultural produce is typical (Hart, 1978; Hewlett, 2017; Yasuoka, 2006).

We obtained raw data on uncalibrated radiocarbon ages from the literature, and calibrated northern and southern hemisphere sites to the IntCal20 and SHCal20 calibration curves respectively, using the R package *Bchron* (Parnell et al., 2008). We checked the agreement of our calibrated dates with those from a recent, comprehensive summary by Clist et al. (2023) (Figs. S1–S2). For each assemblage we produced a mid-age estimate from all available chronometric dates (including C14, optically stimulated luminescence and U–Th series dating), comparable to the median age from a single age estimate or a mean age where an assemblage was constrained by multiple dates. To enable integration with modelled palaeoclimate datasets, mid-age estimates were rounded to the closest 1000-year interval.

For all assemblages retained for analyses, we synthesized the reported composition of stone tool assemblages from the original literature. We examined the diversity and frequency of terms present in the original literature and how they were employed across multiple sites and between authors. We then categorized these datasets to identify evidence for distinct reduction technologies and tool forms informed by both the range of stone tool technologies reported in assemblages from tropical Africa (following (Blinkhorn and Grove, 2018; Niang et al.,

2020) (see SI.1). Due to the nature of analyses to be undertaken, any given artefact form was required to occur in at least 5 different assemblages and where possible rare artefact types were amalgamated into a broader category of artefact type (e.g. Other LCT's) or excluded from the analysis. Similarly, we amalgamated artefact types based on their simplest description to ensure comparability, despite some authors providing higher resolution descriptions (e.g. scrapers includes diverse side/end/convex scrapers). Ubiquitous artefacts that do not offer information on specific reduction practices or use (e.g. unspecified cores, flakes, debris, unspecified retouched pieces, hammerstones) were excluded from the analysis. Cores and flakes from discrete reduction strategies (e.g. blades and blade cores) were combined into single categories. For retouched tools, both the reduction strategy and nature of retouch were recorded as separate elements, so that a backed blade contributes to both the presence of blade production and use of backing retouch. Five discrete core reduction strategies (Bipolar, Blade, Centripetal and Discoidal, Platform, Point) were identified, based on the presence of cores, blanks, or both elements of a reduction strategy. The absence of reports of Levallois technology beyond the site of Shum Laka and Twin Rivers is notable, particularly amongst the earlier Late Pleistocene assemblages, given that they are a typical component of contemporaneous MSA assemblages in adjacent regions (Grove and Blinkhorn, 2020; Niang et al., 2023). Here, Levallois technologies are grouped as part of Centripetal and Discoidal technologies. Retouched tool types retained for analysis include backed/microliths, bifacial retouched pieces, borers, burins, denticulates, notches, retouched points and scrapers; note that this includes both retouch methods that are technologically distinct (e.g. burins) and those which may exist as part of a spectrum of reduction intensity (e.g. scrapers and denticulates). Heavy tools were a frequent and diverse component of Central African stone tool assemblages, which we divided into four categories (Bifacial Foliates, Core Tools, Core Axes and Picks, Other LCTs). This categorisation of stone tool assemblages is advanced as a consistent means to summarize the diversity currently reported in the relevant literature for the purpose of this analysis, not as an idealised typological scheme. Finally, only assemblages with at least two alternate tools forms present were retained for analysis. The final dataset retained for analyses comprises 92 discrete assemblages derived from 35 sites across Central Africa (Fig. 1; Table 1; SI.2).

3. Methods

Our synthesis of hunter gatherer stone tool assemblages and chronometric dating provides a primary means to describe variability in lithic technology and patterns of change through time. We analyze our full dataset, spanning assemblages dating between 230–1 ka, as well as dividing our data between Late Pleistocene and early Holocene assemblages prior to the appearance of ceramics (120 ka to >8 ka; in this dataset, the assemblage of Twin Rivers dated at 230 ka is excluded) and middle and late Holocene assemblages (8 ka and under) for analysis. To augment the study of behavioural and chronometric data, we examine and describe the geographic and palaeo-environmental context of each occupation. We evaluate these spatial parameters using 5 km and 50 km radii from the site location to characterise the immediate and broader logistical landscape in which a site is situated respectively, following (Blinkhorn and Grove, 2021; Timbrell et al., 2022). This helps to tackle issues with the processes of stone tool assemblage formation, which can be considered not only temporal but also spatial palimpsests of activity, subject to biases in recovery. The available archaeological record is therefore determined in part by natural processes affecting the preservation and accessibility of suitable Quaternary deposits as well as by choices made by archaeologists in investigating a given site. Our evaluation of altitude for each site is based upon the 1 km SRTM DEM (Jarvis et al., 2008) from which we also derive an index of roughness of terrain, based upon the energetic costs of human movement in joules per meter (j/m) following (Minetti et al., 2002). In order to examine past climates associated with each occupation we employ published modelled datasets (Krapp et al., 2021). Padilla-Iglesias and colleagues (Padilla-Iglesias et al., 2022a) found that precipitation and temperature seasonality were better predictors of the locations of contemporary hunter-gatherer camps in Central Africa than mean annual precipitation or temperature values. As a result, we selected four bioclimatic variables to capture

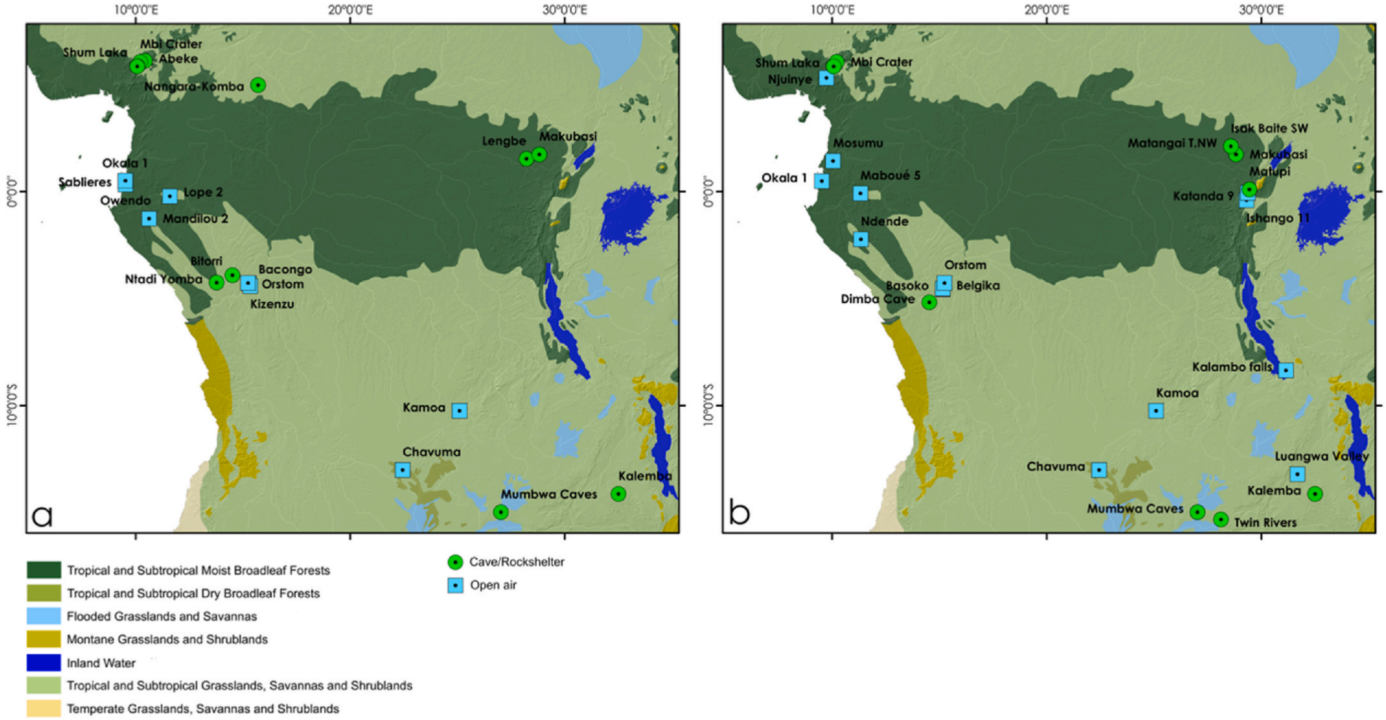

Fig. 1. Map of site locations included in the analyses from a) Mid to Late Holocene (8 ka and younger) and b) Early Holocene, Late and Middle Pleistocene (>8 ka), differentiating open air sites from cave and rockshelter sites.

Table 1
Sites retained for lithic analyses.

Site name	Latitude	Longitude	Site type	Associated publications
Abeke	6.11	10.42	rock shelter	(de Maret, 1982; de Maret et al., 1987)
Bacongo	−4.28	15.27	open air	Lanfranchi and Lanfranchi-Salvi (1986)
Basoko	−4.549	15.151	open air	(Cahen et al., 1983; Cahen and Moeyersons, 1977; de Maret et al., 1977; Van Noten, 1982)
Belgika	−4.53	15.15	open air	(de Maret et al., 1977; Van Noten, 1982)
Bitorri	−3.91	14.50	cave	(de Maret et al., 1977; Emphoux, 1970; Van Noten, 1982)
Chavuma	−13	22.44	open air	(Burrough et al., 2019; Phillipson, 1975)
Dimba Cave	−5.17	14.52	cave	(Cornelissen, 2002; de Maret et al., 1977; Lavachery, 1997)
Isak Baite SW	2.12	28.57	rock shelter	(Cornelissen, 2013; Mercader et al., 2000, 2003; Mercader and Brooks, 2001)
Ishango 11	−0.4	29.3	open air	(Brooks and Robertshaw, 1990; Cahen, 1982; de Maret et al., 1977; Mercader and Brooks, 2001; Van Noten, 1982; Yellen, 1996)
Kalambo falls	−8.35	31.14	open air	(Kandel et al., 2023; Sheppard and Kleindienst, 1996)
Kalemba	−14.12	32.5	rock shelter	(Cornelissen, 2002; Phillipson, 1976a; Phillipson, 1976b; Kandel et al., 2023)
Kamoa	−10.24	25.09	open air	(de Maret et al., 1977; Van Noten, 1982; Muya wa Bitanko-Kamuanga, 1991)
Katanda 9	−0.06	29.36	open air	(Brooks et al., 1995; Feathers and Migliorini, 2001)
Kizenzu	−4.41	15.33	open air	(de Maret et al., 1977; Van Noten, 1982)
Lengbe	1.53	28.21	rock shelter	(Mercader et al., 2000, 2003; Mercader and Brooks, 2001)
Lope 2	−0.22	11.59	open air	(Oslisly, 1992, 1996)
Luangwa Valley	−13.20	31.68	open air	(Barham et al., 2011; Kandel et al., 2023)
Maboué 5	−0.08	11.31	open air	(Assoko Ndong, 2002; Mesfin et al., 2021; Oslisly et al., 2006, 2006)
Makubasi	1.74	28.81	cave	(Mercader et al., 2000, 2003; Cornelissen, 2013)
Mandilou 2	−1.27	10.62	open air	(Clist, 1995; Locko, 1990, 1991)
Matangai Turu NW	2.118	28.573	rock shelter	(Mercader et al., 2000; Mercader and Brooks, 2001)
Matupi	0.1	29.44	rock shelter	(de Maret et al., 1977; Van Noten, 1977, 1982)
Mbi Crater	6.05	10.20	rock shelter	(Clist, 2006b; Essomba et al., 1999; Lavachery, 1997, 1998; Asombang, 1991)
Mosumu	1.43	10.04	open air	(Martí Lezama, 2003; Mercader et al., 2002)
Mumbwa Caves	−14.97	27.02	cave	(Barham et al., 2000; Barham, 2000; Clark, 1942; Kandel et al., 2023)
Nangara-Komba	4.975	15.7	rock shelter	Lupo et al. (2021)
Ndende	−2.23	11.33	open air	(Clist, 1995; Locko, 1989, 1991)
Njuinye	5.31	9.72	open air	(Lavachery et al., 2012; Mercader and Marti, 1999; Mercader and Martí, 2002)
Ntadi Yomba	−4.25	13.77	rock shelter	(Clist, 2006b; de Maret, 1982; Delibrias and Guillier, 1988; Kouyoumontzakis et al., 1985; Lanfranchi, 1990a,b; Van Neer and Lanfranchi, 1985)
Okala 1	0.49	9.51	open air	(Clist, 1995, 1999)
Orstom	−4.27	15.23	open air	(Clist, 1995; de Maret, 1985; Lanfranchi, 1990a,b)
Owendo	0.33	9.52	open air	(Cahen, 1978a; Clist, 1995; Matoumba, 2012)
Sablières	0.51	9.51	open air	(Clist, 1995; de Maret, 1985; Peyrot et al., 1990)
Shum Laka	5.85	10.07	rock shelter	(Asombang, 1988; Cornelissen, 2003; de Maret et al., 1987; Delneuf et al., 1999; Lavachery, 2001; Lavachery and Cornelissen, 2000)
Twin Rivers	−15.31	28.11	cave	Clark and Brown (2001)

differences in site climate: bio01 (mean annual temperature; °C), bio04 (temperature seasonality), bio12 (mean annual precipitation; mm) and bio15 (precipitation seasonality). In order to enhance the resolution of modelled climate datasets, we employed a delta-downscaling approach, whereby the difference between modern and past modelled datasets is applied to a higher resolution modern proxy-derived dataset (Beyer et al., 2020). Finally, we examined the biome4 dataset presented by Krapp and colleagues (Krapp et al., 2021) for evaluation of habitat diversity. We employ these datasets to describe the geography, bioclimate and biomes associated with the mid-age estimate for each stone tool assemblage, calculating mean values across 5 km and 50 km radii for geographic and bioclimatic variables, and proportional values for biome datasets, using the *raster* (Hijmans et al., 2013) and *terra* (Hijmans et al., 2022) packages.

In order to examine the extent to which variability between stone tool assemblages can be explained by the above variables, we calculated dissimilarity matrices for each variable, which constitute all pairwise differences between each assemblage within our dataset. Binary (Jaccard) dissimilarity matrices were calculated for stone tool assemblage composition (hereafter referred to as behaviour) and site type, due to the presence/absence nature of these data, with Manly's metric used for proportional biome data, and Euclidean distances calculated for geographic, bioclimatic, and chronological differences. Cost path distances between sites were calculated based on the 1 km SRTM DEM and employing Tobler's function in the *gdistance* package (van Etten, 2017). For each variable (Site Type, Cost path, Age, Altitude, Roughness, bio01, bio04, bio12, bio15, Biome), we use simple Mantel tests to examine whether there is a significant correlation of between-assemblage similarities in behaviour and between-assemblage similarities in that variable. A common example of the use of this approach is to examine patterns of isolation by distance, for which an increase in the physical distance between sites (here represented by cost path distance) correlates with an increase in dissimilarity for a variable of interest (here, the difference in composition of stone tool assemblages). The underlying null hypothesis across these analyses is that the variable in question plays no significant role in structuring past stone tool assemblages. Variables are retained for further analysis where significant relationships with behavioural distance are recorded. We then employ multiple matrix regressions across variables retained for analysis at each scale (5 km and 50 km radii) to identify which variables show independent, significant relationships with the behavioural dataset. Both simple Mantel tests and multiple matrix regressions were calculated using 9999 permutations to derive *p*-values.

The above analyses determine the effects of the various independent variables on the differences between overall archaeological assemblages. To examine whether these variables significantly influenced the presence or absence of individual technologies within those assemblages, individual binary logistic regressions were performed with the biochem variables (bio1, bio4, bio12, and bio15), mid age, altitude, roughness, and site type as independent variables and each of the technologies as a dependent variable. As the analyses are often imbalanced (e.g., a particular technology may only be present in a small number of assemblages), a weighting scheme was employed to equalize the effects of presences and absences. The weight for an assemblage containing a given artefact type, w_1, depends on the number of other assemblages that contain that artefact, n_1, and is given as $w_1 = \frac{N}{2}n_1^{-1}$, where N is the total number of assemblages in the analysis. Similarly, the weight for an assemblage not containing a given artefact type is $w_0 = \frac{N}{2}n_0^{-1}$. This weighting scheme ensures both that presences and absences have equal total weighting and that the sum of weights across the sample is equal to sample size.

A further issue often encountered when analysing sparse, imbalanced data is that of 'separation', in which regression coefficients fail to converge under maximum likelihood estimation (e.g. Albert and Anderson, 1984; Greenland et al., 2016; Heinze and Schemper, 2002; Kolassa, 1997). To mitigate this issue, penalized logistic regressions using the log-F method of Greenland and Mansournia (Greenland and Mansournia, 2015) was employed throughout. This method uses a weakly informative prior proportional to the log of the F-distribution with one degree of freedom as the penalty term (Greenland and Mansournia, 2015; Rahman and Sultana, 2017) (see Grove and Blinkhorn, 2021 for a recent archaeological application).

Log-likelihoods and deviances as well as chi-squared tests and associated p-values were recorded for each model. The chi-squared test in this case assesses the fitted model deviance against the deviance of a null, intercept-only model whilst taking into account the change in degrees of freedom. To obtain a measure of the proportion of variance explained, a Nagelkerke R^2 value was calculated for each model; this statistic is a revised form of the Cox and Snell R^2 that ensures adequate scaling between zero and one (Cox and Snell, 1989; Nagelkerke, 1991). In addition to full model statistics, significance values for individual coefficients were also calculated; such values were calculated via likelihood ratio tests, which are preferable to Wald statistics when using relatively small sample sizes in penalized logistic regression procedures (Agresti, 2007; Greenland et al., 2016). The individual coefficients of a logistic regression model represent the effect of a one-unit increase in the independent variable on the log-odds of a given technology being present in an assemblage; these coefficients can therefore be exponentiated to give a more intuitive interpretation in terms of the change in odds afforded by, for example, an increase in total annual precipitation of a given number of millimetres. Consideration of odds ratios enables consideration of effect size as well as statistical significance. Despite applying a weighting scheme and employing penalized likelihood functions, some individual models are still regarded as containing numbers of presences too small to yield statistically meaningful results; where this occurred it is noted in the results section below. Analyses were carried out separately for the full dataset, Late Pleistocene and Early Holocene, and Mid-Late Holocene datasets, and separately on data generated via the 5 km and 50 km delta-downscaled analyses.

4. Results

4.1. *Characterizing stone age inhabitations of Central Africa by hunter-gatherer populations*

4.1.1. *Stone tool technologies*

The most commonplace artefact categories are scrapers (present in n = 58 or 63% of assemblages), backed pieces/microliths (n = 58 or 63%) and blade technology (n = 55 or 59.8%), with centripetal and discoidal technology also appearing in half of all assemblages (n = 47 or 51.1%). When ordered by assemblage age, Centripetal and Discoidal Technologies and Backed Artefacts/Microliths appear fairly consistently, whereas blade technologies are notable absent in the few assemblages dating to the end of MIS 5 and in MIS 4, and scrapers, though remaining present, are increasingly rare amongst younger assemblages (Fig. S3). Platform cores (n = 34 or 37%), core tools (n = 32 or 34.8%), point technologies (n = 27 or 29.3%) and borers (n = 31 or 34%) all occur frequently across assemblages, with no obvious chronological patterning. Amongst heavy tools, Core axes (n = 21 or 22.8%) and LCTs (n = 18 or 19.6%) are common and widely distributed through time, with a notable absence of LCTs between the LGM and the early Holocene, whereas bifacial foliates (n = 6 or 6.5%) are rarer and are absent after 14 ka. Bipolar technologies (n = 16 or 17.4%) are the most sparsely represented core reduction technology, and only appear in assemblages up to 8 ka, after which point they are absent. Amongst rarer elements of retouched toolkits, bifacial retouched pieces (n = 16 or 17.4%) are absent until 23 ka, and then present at low frequency, retouched points (n = 15 or 16.3%) mostly appear between either 24–12 ka or 7–3 ka, whilst denticulates (n = 7 or 7.6%) and notches (n = 9 or 9.8%) are particularly sparsely represented in the dataset. Fourteen sites lack diagnostic evidence for core reduction strategies present at the site, potentially indicating a reliance on simple or expedient reduction schemes, site activity not including the full spectrum of lithic reduction and instead focusing on tool use, or the focus of difference archaeologists in defining various aspects of reduction sequences. Notably, eight of these sites do preserve evidence for heavy tool use, the production of which may have played an ancillary role in providing blanks for tool manufacture.

4.1.2. *Geographic and climatic variables*

Unlike previous claims that archaeological evidence for open-air site occupation by hunter-gatherers in tropical forests is virtually absent (Friesem and Lavi, 2017), we found that this was not the case in our dataset, where out of 92 assemblages, 40 were located in open air sites, whilst 52 were located in caves or rock shelters (chisq = 3.756, p = 0.053). Fig. 2 presents the mean altitude, roughness and palaeo-environmental variables from a 50 km radius associated with each Late Pleistocene and Holocene hunter-gatherer occupation within our dataset (SI.3).

Broad continuity can be observed in the mean altitude within a 50 km radius of Central African Stone Age sites between 1660 m and 646 m above sea level, with a notable concentration of sites situated around 400 m above sea level, along with a smaller group of sites occurring 40–50 m above sea level (Fig. 2). Within a 5 km radius, mean site altitudes are broadly continuous from 17 to 1212 m above sea level, with a concentration of occupations at 1535–1544 m, and rare inhabitation of sites up to 2233 m. No distinct chronological patterning is apparent in mean altitude. Similarly, there is considerable continuity in the terrain roughness between approximately two thirds (n = 59) of the sites, ranging between 150 and 210 j/m for a 50 kg individual, with notably rougher terrain in the 50 km radius around the remaining one third (n = 31) of sites of between 245 and 279 j/m. Within a 5 km radius, a comparable pattern is seen, with most sites (n = 68) showing mean terrain roughness values below 240 j/m, and a few sites showing mean terrain roughness values up to 330 j/m. High levels of terrain roughness are associated with higher altitude sites with no discrete chronological patterning apparent.

The average mean annual temperatures within 50 km radii are found within a 10 °C range, between ca. 15–25 °C, with some lower mean annual temperatures down to ca. 12 °C within 5 km radii, but continuously distributed within this range. Increases in mean annual temperature broadly correspond to decreases in site altitude. A notable chronological pattern can be observed with the majority of sites dating within the past 14 ka showing mean annual temperatures within a 50 km radius above 20 °C (49 of 54 sites) whereas the majority of older sites experiencing mean temperatures below 20 °C (32 of 38 sites), with a comparable pattern seen within 5 km radii. All assemblages were found to be associated with relatively high average mean annual precipitation (50 km scale: 851–2557 mm; 5 km scale; 846–2645 mm), distributed as a broad continuum and without any evident chronological structure.

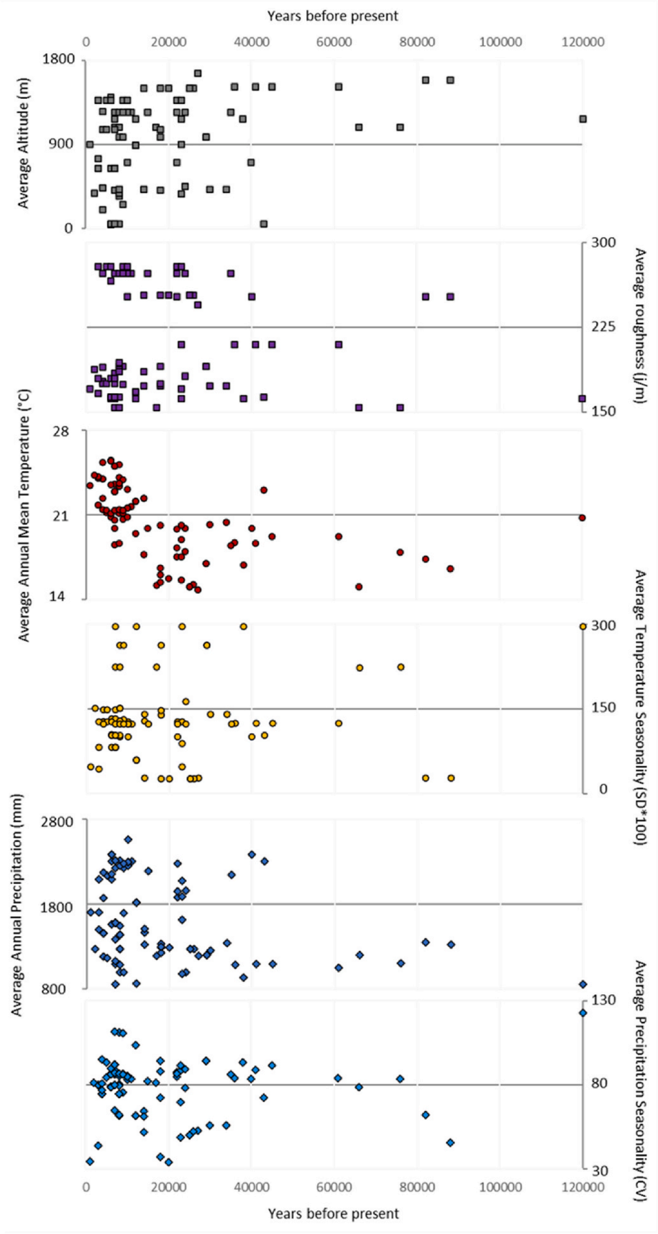

Fig. 2. Average altitude (masl), roughness (m/j), mean annual temperature (°C; BIO01), temperature seasonality (SD × 100; BIO04), annual precipitation (mm; BIO12), and precipitation seasonality (CV, BIO15) within 50 km radius of Late Pleistocene and Holocene hunter-gatherer occupations in Central Africa.

Average temperature seasonality (bio04; standard deviation of the monthly mean temperatures × 100) ranges from 27 to 300 at both 50 km and 5 km scales. The majority of sites (n = 75) have average bio04 values below 166, with a smaller subset of sites (n = 17) with average bio04 values above 223, which are sparsely distributed through time but only apparent up to 7 ka and typically associated with average mean annual temperatures below 20 °C. Average precipitation seasonality (bio 15; coefficient of variation) ranges from 34 to 124 at both 50 km and 5 km scales, with values typically distributed evenly within this range (Fig. 2). Higher precipitation seasonality is typically observed in association with lower mean annual precipitation, with lower precipitation seasonality observed in the middle range of site mean annual precipitation. Precipitation seasonality values > 80 only occur for sites >600 masl, but little clear chronological structure is apparent (Fig. 2).

4.1.3. Biomes

Prehistoric hunter-gatherer inhabitations of Central Africa are most consistently associated with occupation of landscapes dominated by Tropical Xerophytic Shrublands (Fig. 3; SI.3). Tropical Xerophytic Shrubland comprises 100% of biomes within a 50 km radius for 18 assemblages, and over 50% of the landscape for 31 assemblages, with 26 assemblages lacking access to this biome at all. Similarly, at a 5 km scale over half of all sites are dominated by or have access to Tropical Xerophytic Shrubland. At the 50 km scale, landscapes dominated by other habitat types are rare: only 6 assemblages are associated exclusively with Tropical Evergreen Forests; Tropical Deciduous and Tropical Semi-Deciduous forest are associated with 3 assemblages each; two assemblages associated with pure Savanna habitats, and one with Temperate Conifer forests. Tropical deciduous forests (n = 25), Tropical semi-deciduous forests (n = 23), and Temperate conifer forests (n = 21) are most frequently present to some extent within the 50 km radii of sites, whereas Tropical Evergreen Forests (n = 11) and Tropical Savanna (n = 9) rarely feature as part of mixed habitat landscapes.

Distinct changes in habitat composition appear at the end of the Late Pleistocene (Fig. 3; SI.3). Assemblages dating prior to 14 ka are always associated with Tropical Xerophytic Shrublands and Temperate Conifer Forests, with two isolated occurrences of Tropical Deciduous Woodlands associated with occupations dating to MIS 5. Whilst some occupation of Tropical Xerophytic Shrublands is apparent throughout the timeframe spanned by the dataset, Temperate Conifer Forests appear abandoned after 14 ka, coinciding with the earliest occupation of Tropical Evergreen Forests and Tropical semi-deciduous forests. Tropical Deciduous Woodlands become more frequently inhabited from 11 ka onwards, with inhabitation of Tropical Savanna habitats appearing from 8 ka.

4.2. Predictors of toolkit similarity between assemblages

We examined patterns of diversity between stone tool assemblages with regards to differences in chronology, geography, climate and ecology. In order to constrain the impact of the appearance of new patterns of cultural activity, specifically the appearance of pottery at 8 ka and the potential for interaction with farming populations, we split our analyses to span the Full dataset (n = 92), Late Pleistocene and Early Holocene dataset (120–9 ka; n = 54), and Mid-Late Holocene dataset (≤8 ka; n = 37). For each of the three datasets, we performed preliminary simple mantel tests assessing whether each of the selected bioclimatic, ecological and topographical variables predicted similarity in the composition of assemblages, retaining variables with significant relationships to perform multiple matrix regressions. This was undertaken using examining spatial variables at both 50 km and 5 km radii around each site. The summarised results of multiple matrix regressions are shown in Table 2, highlighting the variables that present a statistically significant and independent relationships with variability in stone tool assemblage composition.

Site altitude and site type are consistently associated with variability in stone tool assemblage composition, returning significant results across the three datasets at both 50 km and 5 km resolutions (except in the Late Pleistocene and Early Holocene dataset at 5 km). Precipitation seasonality (bio 15) has a significant and independent relationship with diversity in stone toolkit composition for the full dataset as well as the Late Pleistocene and Early Holocene datasets. For the Mid-Late Holocene dataset at 50 km resolution, mean annual temperature (bio01), provides the only significant bioclimatic variable that correlates with variability across stone tool assemblages, whereas at the 5 km resolution mean annual precipitation (bio12) presents a significant correlation, alongside precipitation seasonality. Differences in biome composition provide significant correlations with stone toolkit composition for the Full dataset, and Mid to Late Holocene dataset at both 50 km and 5 km resolutions, but not for the Late Pleistocene to Early Holocene dataset. Age differences in assemblage provide a significant indicator of variability in stone toolkit composition within the Mid to Late Holocene

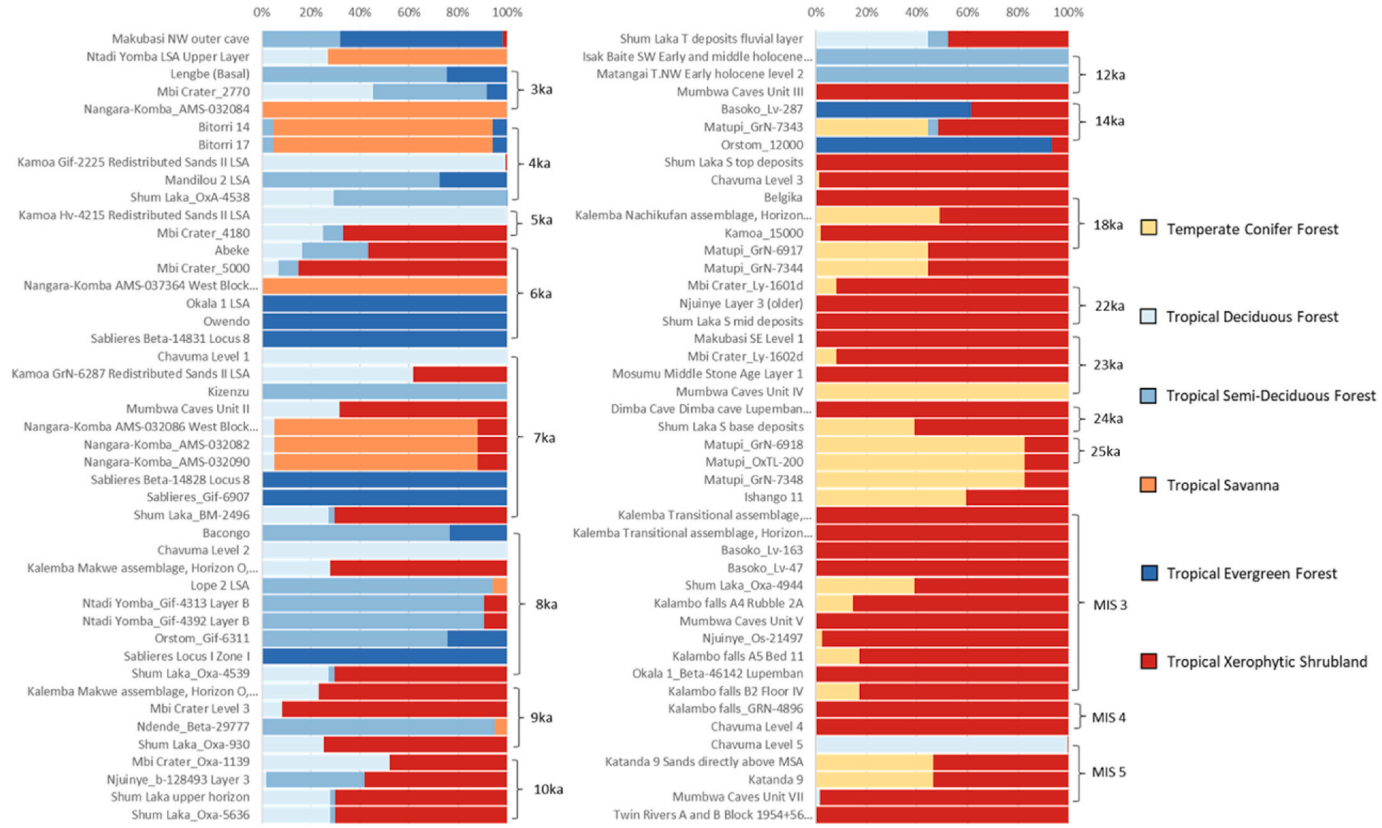

Fig. 3. Proportions of alternate biomes present within a 50 km radius of Holocene (left) and Pleistocene (right) Central African hunter-gatherer occupation sites; age (in ka) or Marine Isotope Stages (MIS) are shown to illustrate the chronology of multiple occupations from a comparable timeframe and illuminate changing biome accessibility through time.

Table 2
Summary of multiple matrix regression estimates where $p < 0.05$ (*), <0.01 (**) and <0.001 (***) based on 9999 permutations and key test statistics.

	Full Data		LP&EH		M&LH	
	Estimate (5 km)	Estimate (50 km)	Estimate (5 km)	Estimate (50 km)	Estimate (5 km)	Estimate (50 km)
Age					0.118**	0.114**
Altitude	0.171***	0.209***		0.209***	0.159**	0.200***
BIO01						−0.187**
BIO12					0.103*	
BIO15	0.111*	0.120*	0.167*	0.192**		
Ecology	0.054**	0.107***			0.078**	0.162**
Roughness				0.054**		
Site type	0.022**	0.016**	0.082***	0.072***	0.062**	0.040*
Multiple R^2	0.088	0.140	0.121	0.167	0.152	0.198
F-Statistic	57.426	84.545	28.048	40.612	14.700	20.227

dataset, whereas terrain roughness only provides a significant correlation within the Late Pleistocene to Early Holocene dataset at a 50 km scale. Notably, costpath distances between sites and differences in temperature seasonality (bio04) did not correlate to patterns of variability within stone tool assemblages.

4.3. *Predictors of individual artefact forms*

4.3.1. *Full dataset*

Within the full dataset, significant models were returned for blades, bifacial retouch, and scrapers at both 5 km and 50 km scales, and for core tools, core axes and picks at the 50 km scale. Total Annual precipitation (bio12) and altitude are the most influential bioclimatic variables in these analyses. At both the 5 km and 50 km scales blades, scrapers and core tools are all more likely to be present in assemblages at higher altitudes. Bifacial retouch is more likely to be present in assemblages receiving higher total annual precipitation, while scrapers are less likely to be present under such conditions.

At the 5 km scale core axes and picks are less likely at lower values of total annual precipitation but more likely under greater temperature seasonality, and core tools are more likely at higher altitudes. These results, however, are not replicated at the 50 km scale. At the 50 km scale both blades and bifacial retouch are less likely in older assemblages, but these results are not replicated at the 5 km scale.

These results are shown in full in SI.6; a brief summary is given in Table 3.

4.3.2. *Late Pleistocene and Early Holocene dataset*

Within the Late Pleistocene and Early Holocene dataset, core tools are more likely to occur at higher altitudes, in younger assemblages, and

Table 3

Significant relationships between environmental variables and individual technologies, as determined by logistic regressions. Only models that achieve overall model significance ($p < 0.05$) are shown. + indicates a positive relationship, - a negative relationship. Nag. R^2 = Nagelkerke R^2 statistic. Symbols in red are those that are significant at both 5 km and 50 km scales for a given technology in a given dataset. For full results and further statistics, including full model significance tests, see SI.6.

	Full Data								LP&EH		
	5 km					50 km			5 km	50 km	
	blades	bifacial	scraper	core tools	coreaxes	blades	bifacial	scraper	core tools	scraper	core tools
BIO01									–		
BIO04					+					–	
BIO12		+	–		–		+	–	–	–	–
BIO15									+		
Altitude	+		+	+		+		+	+	+	+
Roughness											
Site Type									–		
Age						–	–		–		–
Nagelkerke R2	0.287	0.241	0.315	0.222	0.226	0.281	0.226	0.266	0.396	0.325	0.340
Model p	0.004	0.020	0.001	0.033	0.030	0.005	0.031	0.007	0.014	0.049	0.041

when total annual precipitation is lower; this result holds at both 5 km and 50 km scales. At the 5 km scale, results suggest that core tools are also more likely to occur under lower annual mean temperatures, higher values of precipitation seasonality, and in caves and rockshelters as opposed to open air sites. At the 50 km scale scrapers are more likely to occur at higher altitudes and when total annual precipitation and temperature seasonality are lower.

4.3.3. *Mid-Late Holocene Dataset*

No significant models were returned for the Mid-Late Holocene Dataset.

4.3.4. *Evaluation*

In addition to the significant results described in the above sections, a number of other technologies were significantly predicted by various independent environmental variables, but with presences or absences in fewer than 10 assemblages; these sample sizes are considered too small to support adequate statistical inference, but are presented in full in the supplementary materials (see SI.6). The most robust results are those for which the same independent variables have the same effects on the same technologies at both 5 km and 50 km scales. In all cases, such results demonstrate patterns related to altitude, total annual precipitation, or chronology, and involve blades, bifacial retouch, core tools, or scrapers. Throughout the datasets analysed, altitude and total annual precipitation exert the greatest effects on the presence or absence of individual technologies. In the full dataset blades are more likely to occur at higher altitude, bifacial retouch is more likely to occur under higher total annual precipitation, and scrapers are more likely to occur at higher altitude and under lower total annual precipitation, regardless of the scale of analysis. In the Late Pleistocene and Early Holocene dataset, core tools are more likely to occur under lower total annual precipitation and at higher altitude, regardless of the scale of analysis. Although models for the presence or absence of particular technologies identify a considerable number of significant relationships, they often explain a relatively small percentage of the variance in the data. Converting the model coefficients to odds ratios gives a more intuitive picture of the effects of the independent variables. Taking the full dataset as an example, a 100 mm increase in total annual precipitation increases the odds of bifacial technology being present by 6.42% (5 km scale) or 5.66% (50 km scale) and reduces the odds of scrapers being present by 6.55% (5 km) or 5.71% (50 km). A 100 m increase in altitude increases the odds of blades being present by 15.50% (5 km) or 15.69% (50 km) and increases the odds of scrapers being present by 9.42% (5 km) or 6.91% (50 km). For reference, total annual precipitation values in the dataset have a range of 1797 mm (847–2644 mm), and altitude values a range of 2214 m (16 - 2230 m) (values given for the 5 km dataset).

Zooming in further, the model for scrapers (which includes significant effects of both altitude and total annual precipitation) explains only 32% (5 km scale) or 27% (50 km scale) of the variance in the presence of this technology (percentages of variance given are based on Nagelkerke R^2 statistics). This is equivalent to the conclusion that 68% (5 km scale) or 73% (50 km scale) of the variance remains unexplained by the independent variables included in these models. The models for scrapers are at approximately the midpoint of the range of R^2 values recovered by the significant models in our analyses in terms of their ability to explain the variance in assemblage composition (range: 0.22–0.40). The remaining variance is presumably related to variables not included in our analyses, which are likely to include the cultural factors treated in more traditional archaeological analyses such as innovation and diffusion, which together influence the formation and persistence of cultural traditions.

Taking the three analyses (of the Full Dataset, the Late Pleistocene and Early Holocene Dataset, and the Mid-Late Holocene Dataset) together, altitude and total annual precipitation (bio 12) are the two variables that exert the strongest effects on assemblage composition, with other independent variables exerting effects on a lesser number of individual technologies. Altitude and total annual precipitation are also responsible for the majority of the results that hold across both spatial scales. It is perhaps surprising that chronology exerts relatively minimal effects on the presence or absence of particular technologies, but by including it in the analyses we are able to control for those effects, and this makes the influence of other variables more apparent. While chronology and environment may be related (because environments change over time), environmental variation tends to be periodic rather than monotonic, and this allows our analyses to separate environmental effects from those that are simply chronological. The multiple regression format returns partial coefficients (i.e., the effects of each independent variable when the others are held constant), demonstrating that variables such as altitude and precipitation exert effects that are independent of chronology (and of each other). Finally, the lack of significant results in the Mid-Late Holocene dataset may be due to insufficient variance in either the independent variables or in toolkit composition. This dataset covers a much shorter period than either the full dataset or the Late Pleistocene and Early Holocene dataset, and therefore contains less variation in the variables of interest.

5. Discussion

We have presented the first quantitative synthesis of hunter-gatherer stone tool datasets from Central Africa spanning the Middle Pleistocene to Late Holocene, evaluated how assemblages vary with respect to differences in time, space, geography and ecology, and assessed alternate predictors for the presence of individual elements of stone tool kits. Below, we evaluate the outcomes of our analyses, drawing comparisons both to modern hunter-gatherer populations in the region and contemporaneous occupations of tropical Africa.

5.1. Comparisons of tropical african hunter-gatherer site environments

Previous work on tropical rainforest hunter-gatherers across the globe has indicated an almost complete absence of archaeological evidence for open-air site occupation in and around tropical rainforests (Friesem and Lavi, 2017; Scerri et al., 2022). Given that many ethnographic and historical hunter-gatherers in these areas live in open air sites, there has been a debate on whether such contrast is the product of a difference between prehistoric hunter-gatherers who would have differed from contemporary ones and avoided open air sites in tropical forests (Anderson, 1997), research bias or intensive post-depositional processes which would have led to an underrepresentation of open-air sites associated with foragers in tropical forests (Friesem and Lavi, 2017). The fact that our dataset comprised a roughly similar amount of open-air sites and caves/rock shelters is consistent with a niche continuity between prehistoric and contemporary Central African hunter-gatherers.

Our survey of the location of dated hunter-gatherer archaeological assemblages in Central Africa in the Late Pleistocene and Holocene revealed that environmental parameters were comparable to those inhabited by present day hunter-gatherer populations, and share considerable overlap with eastern African MSA populations (Timbrell et al., 2022). The range of altitudes in which our sites were observed was also comparable with that observed within the 20 km radius of the location of the 749 camps from Padilla-Iglesias et al. (2022a), where the median altitude of camps was 445 m above sea level, and most camps were concentrated around the median. The limited range of altitude at which most hunter-gatherers live is perhaps unsurprising given the sharp ecosystem gradients observed with increasing elevation, as well as the physical barriers that mountains present to human mobility (He et al., 2019). In fact, recent research has shown that altitudinal barriers might have been responsible for the divergence of human genetic lineages following the Out-of-Africa human expansion (Delser et al., 2021).

The temperature range at Central African prehistoric hunter-gatherer sites during their occupation associated with each of our assemblages were virtually identical to the temperature range of the locations of 749 camps from contemporary hunter-gatherers in the region reported by Padilla-Iglesias et al. (14–26°C, Padilla-Iglesias et al., 2022a). It was also broadly comparable to that observed in the majority of sites in a recent study of MSA inhabitations in Eastern Africa (9–25 °C), where low mean temperature values were rare and associated with occupation of high, mountainous terrains (Timbrell et al., 2022). The range of mean annual precipitation at the locations of our assemblages was directly comparable to the precipitation range in the locations of the contemporary Central African hunter-gatherer camps compiled by Padilla-Iglesias et al. (1085–2603 mm; Padilla-Iglesias et al., 2022a). Direct overlap is observed between the precipitation experienced in eastern African MSA sites (620–1550 mm; Timbrell et al., 2022) and over half of the Central African sites examined here. Up to 1000 mm more annual precipitation is observed in the remaining Central African sites compared to eastern African MSA sites, though the former typically post-date MSA inhabitation of eastern Africa.

These findings confirm that hunter-gatherers in Central Africa have long been adapted to tropical environments characterized by low seasonality, mild temperatures, and abundant precipitation. They also add to the increasing evidence that contemporary Central African Hunter-Gatherers occupy similar ecological niches to those occupied by their ancestors (Lipson et al., 2022; Padilla-Iglesias et al., 2022a). This is contrary to popular assumptions that contemporary Central African Hunter-Gatherers represent marginalized populations only recently displaced into their current homeland following farming expansions in the region starting around 5000 years ago (in particular those of the ancestors of today's Bantu language speakers) (Bailey, 1991; Blench, 1999; Grollemund et al., 2015; Perry et al., 2014; but see also Bahuchet, 2012; Clist et al., 2023; Crevecoeur et al., 2016).

Our evaluation of biome datasets indicates the significance of drier/open landscapes to prehistoric HGs, but also demonstrates accessibility of closed or forested landscapes within the wider logistical landscape. This accessibility of alternate ecologies may have offered access to varied subsistence (and other) resources. The focus on open habitats with accessibility of forest ecologies in the Late Pleistocene is comparable to patterns observed in contemporaneous eastern African sites, alongside a focus on conifer over broadleaf woodlands (Blinkhorn et al., 2022; Timbrell et al., 2022). Ethnographic accounts of contemporary and historical hunter-gatherer populations inhabiting Central African environments have highlighted the extreme variation in foraging activities and mobility patterns following seasonal fluctuations in the availability of forest resources (Bahuchet, 2021; Ichikawa, 1979; Vallois and Marquer, 1976). Contemporary hunter-gatherers in the region tend to be much more mobile and almost fully reliant on hunting and gathering forest resources during the dry season whilst remaining on the edge of rainforests during the rainy season. Therefore, prehistoric hunter-gatherers could have had similarly seasonal mobility and foraging patterns as they would have inhabited regions with more than one ecosystem available (Lieberman et al., 1993). Whilst inhabitation of ecotone environments appear to have remained an important strategy for hunter-gatherer populations, our results suggest a distinct change and diversification of habitat preferences from the terminal Pleistocene onwards.

Few assemblages are reported in the period spanning the second half of MIS 2, a period of increased environmental instability and fragmentation in the region which could have resulted in a significant population fluctuation (Cornelissen, 2002; Padilla-Iglesias et al., 2022a). This is also reflected in the fact that during this time, we observed an increase in the number of different biomes observed within the radii of archaeological sites (Fig. 3). Interestingly, this coincides with a substantive rise in the mean number of different tool types per assemblage (Fig. S4). This suggests that the contrasts between different biomes could have played an important role in the diversification of toolkits, as different tools would have been required to efficiently forage in each of those environments.

The number of assemblages associated with tropical rainforest biomes dramatically increases after 12 ka. Although we cannot reject the possibility of a switch in habitat preferences by Central African Hunter-Gatherers at the time, there are at least two other factors that are most likely responsible for such an observation. Firstly, following the Last Glacial Maximum, there was a rainforest expansion starting around 17 ka and culminating around 12 ka, which means that such environments would have occupied a greater proportion of Central Africa (Cornelissen, 2002). Hence, a limited occupation of rainforests in Pleistocene Central Africa might have been the result of more restricted opportunities rather than an aversion toward accessing forest settings. Secondly, Pleistocene rainforest refugia are likely situated at the core of the modern forest zone, as well as being associated with upland areas, making archaeological survey and excavation particularly difficult (Blinkhorn et al., 2022; Cornelissen, 2002; Helmstetter et al., 2020). Additionally, preservation of organic material is extremely poor in rainforest soils (Foley, 2018); given the extreme historical reliance of archaeological studies on 14C dating, the dating of older tools in such environments is therefore much more difficult (Foley, 2018; Mercader et al., 2003). Finally, further work evaluating biome4 outputs against regional proxy records (e.g. Lezine et al., 2019) may help to refine characterisations of Central African biomes and ecological change (see Padilla-Iglesias et al., 2022a for an example).

The observed rise in importance of tropical savannas as bridges between broadleaf forests and xerophytic shrublands from 8 ka onwards coincides with first signs of pottery use, and therefore storage in Central Africa (de Maret et al., 1987; Lavachery, 2001), as well as admixture with incoming farming populations (Perry and Verdu, 2017). Interestingly, this period coincides with the maximum extent of rainforest coverage in the Holocene (Cornelissen, 2002). This raises the question on whether these changes could have triggered a switch in ecological preferences or allowed populations to exploit a more diverse set of environments.

5.2. Explaining assemblage scale variability in stone toolkits

Combinations of differences in age, altitude, mean annual temperature (bio01), mean annual precipitation (bio12), precipitation seasonality (bio15), ecology, terrain roughness, and site type explain between 8.8% and 19.8% of variability in stone tool assemblage composition in Central Africa. Difference in altitude between sites presents the strongest means to predict differences in assemblage composition across the full dataset. The absence of independent correlations for temperature, precipitation and roughness within multiple mantel tests despite significant results when individual variables are considered can be best explained by spatial autocorrelation, with altitude typically associated with cooler, wetter and rougher terrains. Altitude gradients have been shown to be key for shaping the patterns of hunter-gatherer mobility elsewhere (e.g. Delser et al., 2021), and the habitability of particular environments by hunter-gatherers. Precipitation seasonality presents the next strongest, independent means to explain differences in assemblage composition, indicating some impact from climatic factors that are not encompassed by spatial autocorrelations, emphasising the importance of seasonal, rather than annual, climate fluctuations for influencing human behaviour. Precipitation seasonality was previously found to be the single best predictor of hunter-gatherer occupation in Central Africa (Padilla-Iglesias et al., 2022a), and our results suggest considerable longevity to its influence on human behaviour in the region. Whilst patterns of past ecology are likely to have been influenced by similar geographic and climatic factors, an independent impact of ecological similarity is apparent on lithic assemblages, potentially indicating that certain constellations of stone tools were employed to tackle particular habitats or resource structures. A similar finding has been obtained when assessing predictors of similarity of the toolkits of contemporary hunter-gatherer populations in the region (Padilla-Iglesias et al., 2022b). A final, independent factor that can explain variability between stone tool assemblages is whether they were recovered from open air or closed (cave or rockshelter) sites. This may result from differences in patterns of archaeological investigation, sediment accumulation and preservation, as well as past differences in human behaviour, which includes different site uses, longevity of occupations forming a given assemblage, as well as how the site was situated for patterns of import, discard, and export of stone tools across the wider landscape.

Further evidence that the toolkit similarity of assemblages found in similar ecologies might be due to convergent evolution is that the cost-adjusted distance (costpath) between sites was not a significant predictor of similarity in toolkit composition across the three datasets. Again, a similar result was obtained in Padilla-Iglesias et al.‘s study on the toolkits of contemporary Central African hunter-gatherers (Padilla-Iglesias et al., 2022b). Importantly, this is in contrast with genetic studies showing that geography is the best predictor of genetic similarity across the African continent prior to agro-pastoralist expansions (Lipson et al., 2022; Vicente and Schlebusch, 2020). The lack of an effect of ecosystem similarity on toolkit similarity in the Late Pleistocene and Early Holocene dataset might be due to the greater overall similarity in the ecosystems occupied prior to the Holocene, which predominantly focus on Tropical Xerophytic Shrubland and Conifer Forests (Fig. 3).

Direct comparisons with comparable analyses in eastern Africa are not straightforward, due to the different range of variables examined (Timbrell et al., 2022), particularly the absence of ecology as well as temperature and precipitation seasonality variables but the inclusion of raw material types, that may offer a further spatially autocorrelated confound. Nevertheless, the significant effect of site type on assemblage composition is highlighted for explaining patterns of assemblage composition, with both a geographic variable (roughness) and a climatic variable (annual precipitation) presenting independent means to explain constellations of technologies with a stone tool assemblage. Building on the results of Blinkhorn and Grove (Blinkhorn and Grove, 2021), our results support the importance of integrating climate model datasets that span the timeframe of interest, rather than characterising climatic extremes, into such analyses. Where this has been the case, both here in Central Africa, and elsewhere in eastern Africa (Timbrell et al., 2022), an independent role for climatic factors has been elucidated, separate from other dominant geographic features of altitude or roughness respectively. However, at least 80% of the variability in stone tool assemblage composition is not explained by the variables studied here. This directly quantifies the scope for alternate factors to influence assemblage composition, including (but not limited to) different patterns of raw material use, culturally mediated technological choices, stylistic variability, potential equifinality in the functional range of alternate tools constellations, as well as the influence of choices made by archaeologists in recovering and reporting stone tool assemblages.

5.3. Predicting the presence of artefact forms

Whilst the above section examines the correlates of overall differences between assemblages, analyses of individual technologies decompose these differences and permit examination of associations between environmental variables and particular technologies. Overall, the results presented above invite three levels of analysis. The first examines the conditions suitable for habitation, identifying the conditions conducive to hunter-gatherer existence in Late Pleistocene and Holocene Central Africa. The second builds on this by examining variation in overall assemblage diversity, identifying variables that structure this diversity within the overall envelope of habitable conditions. The third examines whether particular technologies are associated with particular environmental variables, revealing the finer-scale variation responsible for assemblage-level differences.

The results of Section 4.3 demonstrate that, although relatively few individual technologies demonstrate significant relationships with environmental variables, those models that are significant explain reasonably high proportions of variance in the presence of particular technologies (20–40% based Nagelkerke R^2 statistics). The individual variables having the greatest effect are altitude and total annual precipitation; of the variables considered, only terrain roughness has no effect on any technology at either of the two scales of analysis. As noted above, chronological effects on individual technologies are minimal; within the Late Pleistocene and Early Holocene dataset, core tools are more prevalent in younger assemblages, whereas within the Full dataset blades and bifacial technology are more likely to be present in younger assemblages, but only at the 50 km scale of analysis. In a comparable analysis of eastern African MSA assemblages (Timbrell et al., 2022), only core tools and Levallois flakes were found to show significant chronological variation, with both more likely to be present in older assemblages. At a broader scale, Grove and Blinkhorn (2020; see also Blinkhorn and Grove, 2021) found that LSA assemblages in eastern Africa are indicated by the presence of backed microliths, bipolar technology, and blades, with MSA assemblages indicated by the presence of core tools, Levallois flakes, point technology, and scrapers. The distinction between MSA and LSA, however, is not a strictly chronological distinction, and does not map directly onto the division in the dataset considered above.

It is notable that less than a third of individual artefact forms (5/17; blades, bifacial, scrapers, core tools, core axes/picks) return significant models, but that when they do their R^2 values are considerably higher than those of the whole-assemblage models reported in Section 4.2 (compare R^2 values in Tables 2 and 3). These two sets of analyses are thus fully consistent in suggesting that only certain elements of the toolkit are affected by the variables we consider; these elements are isolated in the results of Table 3, whereas the results of Table 2, employing overall archaeological distances between assemblages, simultaneously analyze both elements that are directly affected by the environment and those that are not. The articulation of environmentally labile technologies with those that do not vary significantly in relation to environments is an interesting area for future study, and invites some tentative explanations for variation unrelated to environmental differences.

Firstly, some artefact forms may show no significant variation with respect to environmental variables because those forms are valuable in multiple environments. Such forms should be present in large numbers of assemblages irrespective of environmental variation; in the current dataset, centripetal and discoidal technologies and backed artefacts/microliths are possible candidates. Secondly, it remains a possibility that certain tool forms were innovated in or transmitted to different regions at different times due to sporadic contact between populations, or that they fell out of use in some regions due either to the stochastic nature of cultural transmission or the presence of alternative innovations. Such tool forms might be expected to show spatio-temporal patterning indicative of inter-populational contact, but such patterning is difficult to detect when employing presence/absence data. The possibility of functional redundancy (i.e., that multiple tools could be used for the same task, with each population therefore employing only a subset of those tools) is important to studies of inter-assemblage variability, but firm conclusions rely on detailed microwear analyses.

Comparison of the results presented here with those previously published on eastern African assemblages (Blinkhorn and Grove, 2018, 2021; Timbrell et al., 2022) are instructive, however, at numerous scales of analysis. Levallois technology is present in the dataset analysed here only at Shum Laka, whereas Levallois flakes, points, and blades are numerous in eastern African assemblages of similar age (Blinkhorn and Grove, 2018, 2021). In general, LCTs and larger, heavier tools are more prominent in the current dataset than in comparable assemblages from eastern Africa. Bifacial foliates are present in five of the assemblages in the Late Pleistocene and Early Holocene dataset analysed here, but are absent from the Mid-Late Holocene dataset, as well as from most comparable eastern African assemblages. Such artefacts are often considered *fossils directer* of the Lupemban industry; the heavy-duty core axes and picks found in many of the assemblages analysed here also accord with a Lupemban designation, as well as previously having been associated with Sangoan assemblages. The Lupemban itself has historically been associated with adaptation to African forests (e.g. Clark, 1965), but this association remains tenuous, with Taylor (2022) noting that “the techno-morphology and proposed function/s of lanceolate points do not link them to any particular palaeoenvironmental profile”. The environments of many of the assemblages analysed here (particularly in the Late Pleistocene and Early Holocene dataset) are dominated by tropical xerophytic shrubland, and in this sense do not differ markedly from broadly contemporary assemblages in eastern Africa (Timbrell et al., 2022).

At a finer scale, comparisons with eastern African data (Blinkhorn and Grove, 2018; Timbrell et al., 2022) reveal a number of differences in both the environmental variables exerting influences and the technologies affected. The analyses of Timbrell and colleagues (Timbrell et al., 2022: see Supplementary Table S3) focused on the eastern African MSA, and considered only the 50 km radius for environmental variables; accordingly, comparisons here concentrate on the full dataset at 50 km. As noted above, the two most important environmental variables in terms of effects on individual technologies within the central African dataset were annual precipitation (bio 12) and altitude. Altitude had limited effect in the eastern African MSA sample; though it was negatively associated with the presence of platform cores, it did not exert the pervasive influence on eastern African assemblages that it does on central African assemblages. Annual precipitation had a wider effect in the eastern African dataset, being negatively associated with the presence of microliths, borers, centripetal reduction, platform cores, and scrapers; in the central African dataset, it is negatively associated with the presence of scrapers and core axes, but positively associated with bifacial reduction in the Full dataset, and negatively associated with the presence of core tools and scrapers in the Late Pleistocene and Early Holocene dataset. The only specific congruence between the two datasets in relation to precipitation, therefore, is the greater likelihood of scrapers in drier environments. More generally, however, the preponderance of negative correlations suggests that in both datasets higher levels of precipitation are associated with lower assemblage diversity (with diversity defined here as the number of technologies present within an assemblage).

In summary, analyses of individual technologies via the logistic regressions reported in Section 4.3 suggest that within Central African assemblages with greater technological diversity exist at higher altitude and under lower levels of annual precipitation; the latter result is mirrored, though in relation to different specific technologies, in eastern Africa. There are some chronological trends, but whilst these are statistically significant, they are associated with limited effect sizes. Bifacial foliates are present before the 8 ka threshold – albeit in only 9% of assemblages – and absent after it. The greatest difference between central and eastern African assemblages of broadly similar chronological age is the almost complete absence of Levallois technology in the former dataset.

6. Summary

Our work provides the first comprehensive synthesis and quantitative analysis of chronometrically dated prehistoric hunter-gatherer stone tool assemblages from Central Africa. By engaging with climate model outputs, we are able to characterise the past environments and ecologies inhabited by hunter-gatherer populations and integrate these with modern geographic data to explore how site environment preferences changed through time. These analyses, undertaken at a broad spatio-temporal scale and with a concomitantly coarse resolution in terms of both chronology and typology, provide a comprehensive baseline for the study of Central African Late Pleistocene and Holocene hunter-gatherers. We hope that this synthesis will prompt others to examine the conclusions it proposes at finer on-site and between-site scales, albeit with the necessarily smaller sample sizes that such analyses must employ. Analyses of tool frequencies, full reduction sequences, and technological or attribute analyses all have the potential to add to the overall patterns elucidated above, and more detailed examinations of subsets of the large number of assemblages employed here should ultimately provide a more nuanced picture of the interaction between bioclimatic variables and prehistoric hunter-gatherer behaviour. As highlighted above, we have developed a series of statistically significant and highly informative explanatory models, but in most cases these explain relatively small proportions of the variance in overall assemblage composition; future analyses should focus on examining the cultural processes that are likely to explain the remainder.

Most notable within the results reported above is a discrete change in ecological landscape occupied by hunter-gatherers, from those dominated by tropical xerophytic shrublands with access to conifer forests to those comprised of more mosaic savannah and broadleaf forest habitats from around 14 ka, broadly contemporaneous with a shift to occupation of notably warmer landscapes. These characterisations of past landscapes in turn enable us to examine the extent to which differences in time, space, geography, climate and ecology can explain variability in the gross composition of stone tool assemblages, as well as predict the presence or absence of individual assemblage components. Our results highlight the significant impact that site altitude has both on the overall constellation of stone tool assemblages and the presence of specific tool forms, as well as the important role of precipitation seasonality on toolkit composition and mean annual precipitation on the appearance of particular technologies. Extensive comparability is observed in the landscapes inhabited by past and present hunter-gatherer populations in Central Africa as well as the variables which appear to influence patterns of site distribution. This supports a long-standing pattern of forager engagement with regional habitats that may not have been as substantively modified by the expansions of farming populations as previously anticipated.

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Author contributions

C.P.I, M.G and J.B conceptualized the project. C.P.I compiled the data. M.G and J.B analysed the data. All authors wrote the paper, verified the findings and approved the final version of the manuscript.

Declaration of competing interest

The authors declare they have no competing interests.

Data availability

All data and code required to reproduce the results reported in the manuscript are available on this link: https://www.dropbox.com/sh/27j8xp3kz41wrgl/AADYTyO76lGXgLk3cL9bNnexa?dl=0.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2023.108390.

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